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LAGODON RHOMBOIDES (LINNAEUS)

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ENERGY REQUIREMENTS OF A POPULATION OF PINFISH *LAGODON RHOMBOIDES* (LINNAEUS)¹

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Abstract. Biomass and rates of metabolism were estimated for a population of pinfish in the Newport River estuary, North Carolina. This information was used to estimate the routine energy requirements of the pinfish population and to relate these energy requirements to primary productivity in the estuary.

Population estimations of larval, juvenile, and adult pinfish were made over a 2-yr period. Peak biomass occurred during March-April when both larval fish and juvenile-adult fish were at maximum numbers.

Routine metabolism was measured at 10° and 15° C for larval fish and at 5°, 10°, 15°, 20°, and 33° C for juvenile-adult fish. Metabolism-weight coefficients calculated from the data for juvenile-adult fish were lower than values for pinfish reported by other investigators.

The yearly routine energy requirement of the pinfish population was estimated to be 1.1×10^6 calories. This annual requirement was compared to total estuarine primary productivity with the assumption of 10% and 20% net growth efficiency for the estuarine system. At 10% efficiency the pinfish would require 0.9% and at 20% they would require 0.4% of the total energy available to secondary consumers.

Key words: Biomass; energy requirements; metabolism; oxygen consumption; pinfish; temperature.

INTRODUCTION

An understanding of the production potential of a fish population requires measurement of energy requirements of the population in relation to total energy available. Early investigations of fish populations dealt primarily with standing crop. It is now possible to estimate energy requirements of individual fish and in theory to calculate the energy requirement of the population. In fact, however, it is usually difficult to obtain all of the data needed for these calculations.

Difficulties in measuring the necessary population parameters have limited the number of studies to determine the metabolic requirements of fish populations in relation to ecosystems (Mann 1965, 1969). Fewer studies have been conducted on the energy requirements of marine species than of fresh water species because population numbers fluctuate greatly in relatively short periods of time in marine and estuarine environments (Mann 1969). Early attempts to describe marine ecosystem dynamics were made by Clarke (1946) and Harvey (1950), who used commercial catch records and data collected by other investigators to estimate growth and food requirements of fish.

In this investigation, the routine energy requirements of a population of pinfish (*Lagodon rhomboides*) were studied as part of a larger investigation attempting to model trophic level energy relationships

in an estuarine ecosystem near Beaufort, North Carolina. Specifically, the effects of normal environmental temperatures on the routine metabolism (oxygen consumption) of various size classes of pinfish held in the laboratory were determined. These data, along with information on the seasonal abundance and biomass of the size classes, were used to estimate energy required for routine metabolism by the pinfish population in the Newport River estuary.

DESCRIPTION OF NEWPORT RIVER ESTUARY

The Newport River estuary, located between Morehead City and Beaufort, North Carolina (Fig. 1), is a relatively small (31 km²), shallow (average depth at low tide, 1.0 m), but productive estuary fairly typical of estuaries found along the North Carolina coast. The primary source of fresh water in the estuary is the Newport River, although some exchange may occur through canals leading to the Neuse River. Salinities are lowest in winter and highest in summer. At a station in the lower part of the estuary (Fig. 1) salinities ranged from 14‰ to 35‰ and temperatures from 2° to 31° C (Table 1). Tide range is highest near the mouth of the estuary (mean 0.8 m) and decreases inland (Thayer 1971). Tides and wind action create currents sufficiently strong to mix the water and minimize vertical stratification (Williams 1966). Bottom sediments range from firm shell and sand in parts of the lower estuary to finer sands, silts, and clays toward the middle and upper reaches.

Animal production in this estuary is supported

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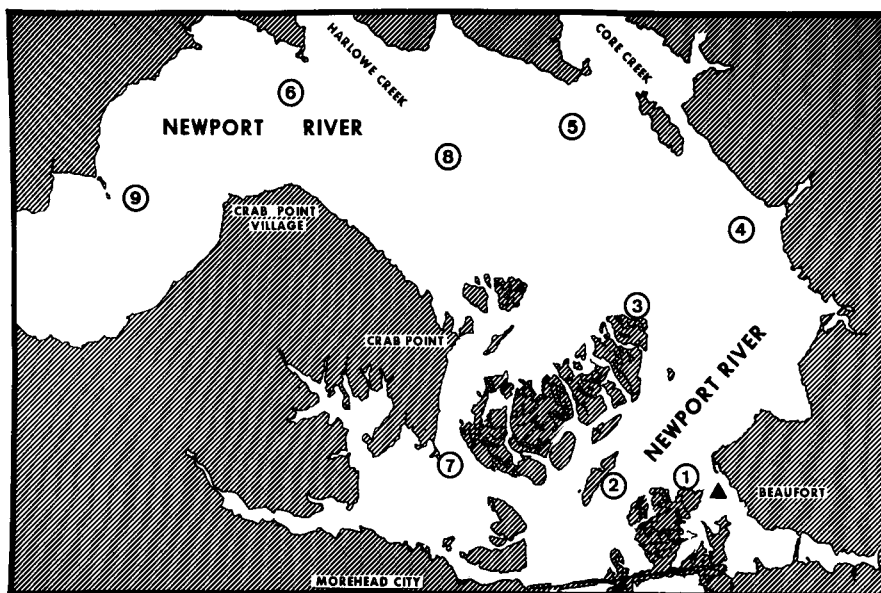


FIG. 1. Newport River estuary showing location of fish traps (circles) and salinity-temperature station (triangle).

mainly by phytoplankton, cord grass, and submerged grasses. Living cord grass and submerged grasses are not eaten directly by organisms but are consumed as detritus.

Previous surveys of fish in the Newport River estuary revealed that Atlantic croaker (*Micropogon undulatus*), spot (*Leiostomus xanthurus*), pinfish (*Lagodon rhomboides*), and Atlantic menhaden (*Brevoortia tyrannus*) were among the dominant species (Turner and Johnson, *in press*).

The pinfish was selected from this group for further study because much information already exists on its range, life history, and metabolism. The pinfish, found from Cape Cod, Massachusetts, to Yucatan in Mexico, is numerically abundant throughout its range, and is tolerant of a wide range of environmental conditions. The life history of pinfish from Florida has been described by Caldwell (1957) and Hansen (1969), and metabolism of pinfish in Texas has been investigated by Wohlschlag and Cameron (1967), Wohlschlag et al. (1968), and Cameron (1969). Thus, results obtained in this study could be compared to those from other geographical areas.

PINFISH POPULATION ESTIMATION

Juvenile-adult fish

Pinfish were captured in modified crab pots. The location of the traps in the estuary (Fig. 1) was based on data obtained in a bottom trawl survey which showed that pinfish did not occur to any extent above station 9. The fish traps were checked

and baited daily during each survey. At the time of capture, the total length (TL) of each fish was recorded and each was marked by removal of the anal fin prior to release. Previous experiments, conducted in the laboratory, indicated that such removal did not cause a significant increase in mortality. Darnell and Wissing (*in press*) also found that clipping the anal fins of pinfish produced little mortality.

The method of capturing the fish by traps did not provide sufficient fish for a Peterson type of population estimation, where all the fish must be marked at one time. Therefore, a multiple census method proposed originally by Schumacher and Eschmeyer and described by Ricker (1958) was used. In this method $P = \Sigma AB^2 / \Sigma BC$, where P is the abundance of the population, A is the number of fish each sample, B is the total number of marked fish released, and C is the number of marked fish collected in each sample.

Unrealistically low population estimates during the initial sample period indicated that the traps were not sampling the entire 31-km² area of the estuary and that a correction factor for area fished was necessary. Five traps were placed at different distances from one another in the estuary to determine the area sampled by each trap. Fish captured at each trap were given distinctive fin clips and a short-term mark-and-recapture study was conducted. Seventy-five marked fish were recaptured, 83% of them at their original location. Only 8% of the fish moved more than 90 m from their original capture site, suggesting that the effective trapping radius

TABLE 1. Average monthly temperature and salinities in the lower Newport River Estuary, N.C. (Fig. 1)

Month	Temperature (°C)			Salinity (‰)		
	\bar{x}	Range	SD	\bar{x}	Range	SD
1969						
October	19.9	15–23	2.22	24.78	18–33	3.06
November	14.1	8–19	2.35	25.57	19–30	2.46
December	9.9	6–15	1.61	29.05	20–34	2.28
1970						
January	6.4	2–13	2.37	26.36	15–34	3.29
February	9.7	8–14	1.30	25.31	14–35	4.21
March	12.3	10–15	1.30	24.89	16–31	3.30
April	17.6	— ^a	2.80	25.48	— ^a	3.47
May	22.2	18–25	1.47	27.29	18–32	3.02
June	25.8	23–30	1.71	27.40	19–33	1.92
July	28.4	26–31	0.82	29.98	26–33	2.30
August	27.9	26–29	0.67	29.72	20–34	1.97
September	27.8	24–30	1.21	30.03	25–33	1.72

^a Data not available.

of a single trap was approximately 90 m. Population estimations (P_t) were adjusted accordingly: $P_t = A_e P_e / A_t N_t$, where A_e is the area of the estuary, P_e is the calculated population, A_t is the area fished by one trap, and N_t is the number of traps fished.

The juvenile-adult portion of the pinfish population was estimated during winter, spring, summer, and fall periods (Table 2). During the winter months, however, insufficient numbers of pinfish were captured for a population estimate. Juvenile-adult pinfish were most numerous in April, when 11–13 cm fish dominated the catch. The May–October estimates showed a continuing decline in mean bimonthly numerical abundance (Table 2). This pattern of a high spring population followed by a decreasing population the rest of the year agreed with previous work in Florida (Caldwell 1957) and Texas (Cameron 1969).

Larval fish

The monthly abundance of larval pinfish was estimated from catches in nets set in the channel under the Pivers Island Bridge near Beaufort. Previous sampling by biologists at Beaufort has shown that approximately one-ninth of the larval fish that entered the Newport River pass through the channel

under the Pivers Island Bridge (R. B. Lewis, Atlantic Estuarine Fisheries Center, Beaufort, N.C. 28516, *pers. comm.*). Using unpublished records for the 1969–70 season and correcting for percentage of area sampled, I was able to make an approximation of the monthly abundance of larval pinfish.

Larval pinfish were collected from November through April with the peak in February and March (Table 3). The size of the larval fish entering the estuary remained fairly constant between November and April, indicating that fish were spawning in off-shore waters during this time. Estimates from previous years showed similar trends, with most larvae entering during late winter and early spring.

METABOLISM

I measured the routine metabolism (Beamish and Mookherjee 1964) of juvenile and adult pinfish in a flowing water respirometer modified from Hoss (1967). The respirometer consists of a reservoir with heating, cooling, and aeration apparatus, a respirometer tank, a constant-level tank, flow meters, and respiration chambers. Water flowing from the respiration chamber passed through the flow meter and sample jar and returned to the reservoir. The rate of flow of water through each respiration chamber was controlled by a valve connected to a

TABLE 2. Estimates of the number of juvenile and adult pinfish in the Newport River Estuary, N.C.

Sample period	No. of fish marked	Size range (cm)	Population estimation	Estimation adjusted for area fished
May–June	1,198	3.5–17.9	9,355 ± 1,574 ^a	1.2 × 10 ⁶
July–August	542	5.5–18.9	2,303 ± 589	4.6 × 10 ⁵
September–October	487	2.5–18.4	1,823 ± 262	4.3 × 10 ⁵
April	622	7.0–20.9	17,302 ± 512	2.3 × 10 ⁶

^a 95% confidence limits.

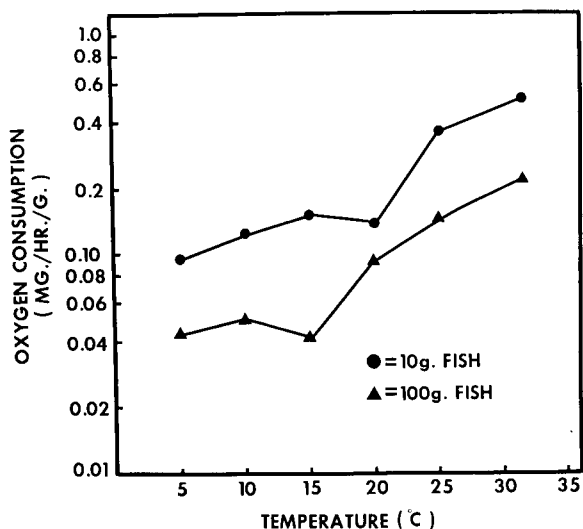


FIG. 2. Calculated oxygen consumption (mg/hr·g) 10-g and 100-g pinfish at various temperatures. Oxygen consumption values calculated by laboratory determined metabolism-weight coefficients for the appropriate temperature.

flow meter, and the oxygen content of the water was measured polarographically. The amount of oxygen used by each fish was calculated by multiplying the difference in oxygen content of the inflowing and outflowing water by the flow rate.

In all cases, the experimental fish were not fed for 24 hr prior to entrainment in the respiration chamber and were acclimated to the respiration chamber for 24 hr before the first oxygen measurement was made. The volume of the respiration chamber was at least 10 times the displacement volume of the fish. Five consecutive measurements of oxygen consumption at 1-hr intervals were made for each fish, and no fish was used more than once. Oxygen consumption measurements were made between 0900 and 1600 hr. Wet weights of the fish were obtained after the last oxygen measurement.

Because of the small size of the larvae I could not obtain oxygen consumption measurements on individuals in the flowing water respirometer. Therefore, I measured oxygen consumption of larval fish in a

TABLE 3. Estimates of the number of larval pinfish in the Newport River Estuary, N.C.

Sample period	Number of larval fish	Size range (mm)
November 1969	1.5×10^6	13–15
December 1969	35.1×10^6	10–18
January 1970	17.5×10^6	17–18
February 1970	221.2×10^6	10–23
March 1970	248.8×10^6	11–24
April 1970	2.5×10^6	12–20

TABLE 4. Summary of oxygen consumption data on larval, juvenile, and adult pinfish

Temperature (°C)	No. of fish	Weight range (g)	a	k	SE of k
33	35	7–40	1.185	0.634	0.0855
25	65	5–63	0.944	0.589	0.0419
20	42	5–67	0.201	0.833	0.0582
15 ^a	55	0.02–0.10	0.264	0.865 ^a	0.0826
15	40	5–98	0.552	0.434	0.0526
10 ^a	54	0.02–0.05	0.393	1.122 ^a	0.1235
10	69	5–59	0.297	0.614	0.0519
5	26	5–48	0.203	0.661	0.1042

^a Larval fish.

differential respirometer. The difference in oxygen consumption as measured by these two methods is not expected to be greater than 20% (W. F. Hettler, Jr., Atlantic Estuarine Fisheries Center, Beaufort, N.C. 28516, *pers. comm.*).

Larval fish were not fed for 24 hr before being placed in the respiration chamber and acclimated in the respirometer flasks for 2 hr. Four consecutive measurements of oxygen consumption were made at 1-hr intervals thereafter. Oxygen consumption measurements were made between 0900 and 1600 hr. Wet weights were measured after the last oxygen measurement.

Seasonal measurements of routine oxygen consumption were made at 10° and 15° C for larval fish and at 10°, 15°, 20°, and 25° C for juvenile-adult fish. These temperatures correspond to the average environmental temperature for the time of year the fish were caught. Oxygen consumption of juvenile-adult fish also was measured at 5° and 33° C even though water temperatures in the Beaufort area do not remain at these extremes for any length of time. Measurements made at 5° and 33° C were not used in the final calculation of the energy requirements.

The relationship between wet weight and metabolic rate was used to calculate energy of metabolism for fish of different weights: $Q = aW^k$, where Q is the rate of metabolism, W is the weight of the fish, and a and k are constants for the species obtained from least-squares regression lines of oxygen consumption on weight (Winberg 1956).

The constant k for larval fish at 15° C was 0.865; at 10° C it was 1.122. Values of k for juvenile-adult fish ranged from 0.43 at 15° to 0.83 at 20° C (Table 4). The relatively low juvenile-adult k value obtained at 15° C and high juvenile-adult k value obtained at 20° C may be due to the variable temperature conditions that occur at Beaufort in spring and fall, when these measurements were made. Wohlschlag et al. (1968) also attributed some inconsistencies in respiration data on pinfish to a seasonal environmental

variation in temperature. During the summer and winter months temperatures tended to be stable for longer periods of time. The number of consecutive days at either 15° or 20° C is much less than at 10° or 25° C, and therefore the fish have much less time to fully acclimate to these temperatures.

The metabolism-weight coefficients (k) for juvenile-adult pinfish ($\bar{k} = 0.63$) are, for the most part, lower than those reported for fish in general (0.67–0.80) by Winberg (1956). Cameron (1969), working with pinfish at approximately the same temperatures, observed higher fall and winter metabolism-weight coefficients (1.13 fall and 1.19 winter). My values for larval pinfish, on the other hand, are higher than Winberg's overall range of values. These discrepancies probably result in part from the weight range of fish used. Cameron (1969) used fish ranging from 1.5 g to 34.9 g (average of 9.5 g). I used fish weighing from 5 g to 89 g (average of 24.8 g). In studies with Atlantic croaker and pinfish, I found that the slope of the calculated regression line for 0.01–0.14 g croakers at 20° C was 1.12 and the slope for 10–100 g fish was 0.57. However, when the data were pooled and a single line calculated for a weight range of 0.01 to 100 g, I obtained a value of 0.78, which is not dissimilar to the universal metabolism-weight coefficient of 0.8 (Winberg 1956). Wohlschlag and Cech (1970) also found a difference in respiratory metabolism between size groups. However, when they combined the respiration data, metabolism conformed to Winberg's values.

The differences in the metabolism-weight coefficients also may result from the type of respirometer used and the length of the acclimation period in the respirometer. Cameron (1969) suggested that his higher-than-expected metabolism-weight coefficients for fall and winter pinfish may have been due in part to the size of the container relative to the size of the fish. He acclimated his fish for only 1 hr, whereas my juvenile-adult fish were acclimated 24 hr. When a fish is first placed in a respirometer its oxygen consumption increases (Keys 1930, Hickman 1959, Mann 1965), then decreases over a period of time until a relatively steady level is reached. Oxygen consumption measurements made in a closed system, with only a short acclimation period, therefore tend to give higher oxygen consumption rates.

Surprisingly, Wohlschlag and Cech (1970) found that large pinfish had a higher rate of metabolism at low temperatures than had smaller pinfish, although the reverse was true at higher temperatures. In my experiments the smaller the fish, the higher the rate of metabolism throughout a temperature range of 5°–33° C (Fig. 2). I did not find a meta-

bolic depression at the highest temperature as reported by both Cameron (1969) and Wohlschlag and Cech (1970), and, in general, the rate of metabolism for both small and large fish increased with temperature up to 33° C.

In Wohlschlag and Cech's study, fish were acclimated to low temperatures for only 3 days over 5° C ranges. My pinfish were naturally acclimated to low temperature. Thus, the difference in acclimation time may account for the difference in respiration rate between large and small fish. Longer acclimation of the fish by Wohlschlag and Cech probably would have resulted in a depression of the metabolic rate of the larger fish.

Winberg (1956) suggested that routine metabolism should be doubled in order to estimate normal metabolism under field conditions. Recent observations by Hettler and Hoss (1971), however, suggest that pinfish routine metabolism measured in the respirometer described in this paper may be a good estimate of normal metabolism. In their experiments the amount of oxygen consumed by a group of pinfish held in a flowing water respirometer was compared to the amount of oxygen consumed by a group of pinfish swimming in a sealed 200-liter circular tank. Salinity, temperature, flow rate, percentage oxygen saturation, and treatment of fish were the same for both systems. Comparisons were made at 15° and 19° C and in both cases oxygen consumption per unit weight was approximately the same. Edwards et al. (1969) concluded that higher metabolic rates measured in fish in large tanks were due to higher rates of feeding rather than increased physical activities. Additional research in this area is needed, but these experiments suggest that, for the pinfish, normal metabolism may be nearly the same as routine metabolism. Therefore, I did not feel it would be justifiable, at this time, to double the routine metabolic measurements in order to calculate energy requirements.

BIOMASS AND ENERGY REQUIREMENTS

Biomass estimates were obtained from population estimates, size structure of the population, and length-weight relationship of the pinfish. The length-weight relationship for juvenile-adult fish was $W = 0.0098 \text{ TL}^{3.17}$ (315 fish) and for larval fish was $W = 0.0089 \text{ TL}^{2.84}$ (49 fish), where W = wet weight and TL = total length. For each population estimate the juvenile-adult fish were separated by length into 5-cm-length classes, and the biomass of each group was calculated by the length-weight formula. I then converted biomass to calories using a conversion factor of 1,160 cal/g wet weight for adults and 672 cal/g wet weight for postlarvae (Thayer et al. 1973).

Energy requirements of the fish population were

TABLE 5. Bimonthly estimate of the biomass, energy content, and energy requirements of the Newport River pinfish population. Data collected over 2-yr period

Date and life stage	Biomass (Kg wet wt.)	Energy content (cal.)	Energy requirement (cal.)
July–August			
Larval	0	0	0
Juvenile-adult	13.4×10^3	14.7×10^9	15.1×10^9
September–October			
Larval	0	0	0
Juvenile-adult	9.7×10^3	10.7×10^9	11.9×10^9
November–December			
Larval	33.0×10^2	2.2×10^8	3.9×10^8
Juvenile-adult ^a	2.4×10^3	2.7×10^9	1.4×10^9
January–February			
Larval	3.2×10^3	2.1×10^9	3.8×10^9
Juvenile-adult ^a	2.4×10^3	2.7×10^9	1.4×10^9
March–April			
Larval	3.3×10^3	2.2×10^9	7.1×10^9
Juvenile-adult	68.9×10^3	75.9×10^9	28.4×10^9
May–June			
Larval	0	0	0
Juvenile-adult	37.0×10^3	40.8×10^9	42.0×10^9

^a Calculated from the September–October population estimate.

estimated in the following manner: (1) the length-weight relationship was used to calculate the average wet weight of the fish (W); (2) wet weight in grams (W) was used in the metabolism equation ($Q = aW^b$) to calculate the amount of oxygen consumed (Q) by an individual fish at a specific temperature; (3) the mg O₂ used per hour per fish was multiplied by the total number of fish; (4) steps 1 through 3 were repeated for each 5-cm-length group, and the oxygen consumption for all classes was summed to give the total respiration for that population estimate; (5) the oxygen consumption of the population was converted to mg O₂ per day and then to calories per day by means of the oxycaloric equivalent, 3.36 cal/mg O₂ (Phillipson 1966); (6) calories per day were multiplied by the number of days in a sample period to give calories per sample period. This procedure was repeated for each population estimate and summed to give the yearly energy requirements of the pinfish population.

The winter population of juvenile-adult fish was estimated from the September–October population since no samples were made in November and December. Trawl samples and limited capture in fish traps showed that the winter population was made up primarily of individuals less than 10 cm. Therefore, I assumed that (1) the portion of the September–October population 10 cm or less would approximate the winter population; (2) negligible growth of pinfish occurs during the winter (Hildebrand and Cable

1938, Caldwell 1957); and (3) no movement of juvenile fish takes place. My population estimations were not made in the same year; thus I had to assume for calculating purposes that the pinfish population did not vary significantly between years, and I pooled the various monthly population estimations to obtain a yearly estimate.

Biomass levels and the energy requirements of the pinfish population were greatest during spring and summer and least during fall and winter (Table 5). Peak biomass and energy content occurred during April, when both larval fish and juvenile-adult fish were at peak numbers. Energy required for metabolism was greatest during the May–June period, when the water temperature had increased from an average of 15° C to an average of 24.0° C, resulting in increased oxygen consumption by the fish. Biomass, energy content, and routine metabolism decreased during July–August and September–October. The seasonal low in fish abundance occurred in September–October, but I estimated that the minimum biomass, energy content, and energy required for routine metabolism occurred in November–December (Table 5). During this period the water temperature reached a mean low of 10° C; the numerical abundance of juvenile-adult fish was greatly reduced; and these fish generally were less than 10 cm total length. Larval fish were starting to enter the estuary at this time and did not reach their peak for another 2 mo.

The pinfish population required approximately 1×10^{11} calories for routine metabolism during 1969 and 1970 (summation of last column, Table 5). Total energy requirements were highest in the May–June and lowest in the November–December sample period. The time of maximum energy requirement coincides with a period of increased production in the estuary (Williams 1966, Thayer 1971) associated with rising water temperatures. As the season progressed the energy requirements of individual fish increased because of increased water temperatures, but the total energy required by the population decreased because larger fish migrated out of the shallow estuary in response to the increase in water temperatures (Wohlschlag et al. 1968, Darnell and Wissing, *in press*) (Table 1). During November–December only a remnant of the pinfish population remained in the estuary and total energy requirements were at a minimum. In general, the pattern of movement of the fish in the Newport River estuary was similar to that described by Caldwell (1957) for estuaries in Florida and by Cameron (1969) for estuaries in Texas.

To relate the energy required by the pinfish to the energy produced in the system, I assigned the fish to the second consumer level of the food chain.

This decision was based on observations by Caldwell (1957) and Darnell (1958) and on observations I have made on pinfish collected at Beaufort. Using data collected by Williams (1966) and Thayer (1971), I estimated annual average net production of phytoplankton in the Newport River estuary as 35.0×10^{12} calories per year. Assuming that for the estuarine system near Beaufort the contribution of phytoplankton, submerged aquatic plants, and marsh grass are in the order of 53.7%, 45.9%, and 0.4%, respectively (Wolfe, *in press*), the primary production available to consumers would be 65×10^{12} calories. If the Newport River ecosystem has an ecological efficiency of 10% (10 g of plant production is required to produce 1 g of herbivore at trophic level 1.0, and 100 g of plant production is required to produce 1 g of carnivore at trophic level 2.0) the secondary consumers, including pinfish, would have 10% (6.5×10^{12} calories) of the total primary production available to them as a source of energy (Phillipson 1966). Thus, for routine metabolism (1.1×10^{11} calories), the Newport River pinfish population would require 1.7% of the total yearly energy available to secondary consumers, or about 0.2% of the total primary production.

Calculations made by Williams (R. B. Williams, Biological Oceanography Program, National Science Foundation, Washington, D.C. 20550, *pers. comm.*), however, suggest that the ecosystem in the Beaufort area must be more than 10% efficient because the plant production demanded by a 10% efficiency drastically exceeds observed productivity. Williams believes that the overall ecological efficiency in this type of estuarine ecosystem is probably nearer 20%. Slobodkin (1962) also concluded that ecological efficiency would fall between 5% and 20%. If the efficiency of the Newport River ecosystem is 20% the pinfish population would require only 0.9% of the total yearly energy available to secondary consumers.

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